Habitus

This species is a slender form, which varies in size at maturity, but most individuals are about 10 mm. long, with some attaining 15 mm. Figure 1 depicts a living animal crawling on a flat surface. The rhinophores are held out laterally at a slight angle to the substrate. The anterior margins of the foot are extended on the surface and can be seen dorsally. The plump cerata are held curved dorsally over the back, at times interdigitating, but when the animal is disturbed they are extended out straight, giving a "bushy" appearance. To the unaided eye most individuals appear uniformly black except for the whitish rhinophore and cerata tips. The intensity of pigmentation of all parts of the body varies greatly in the local populations, and examination of large numbers of individuals reveals much variation. Some individuals are intensely pigmented so that even the white areas appear dark grey. Other individuals are so lightly pigmented that the animals appear brownish or even yellowish due to the color of the gonad. In many of the very lightly pigmented animals the usual pigment pattern becomes further obscured since the cream-colored areas do not contrast strongly with the darkly pigmented areas, just as it is obscured in dark forms by the light areas being invaded by dark pigment. The pattern described here is that of individuals in which the contrast is most distinct.

External Morphology

The cerata are not scattered but arise from two well-defined dorso-lateral zones. They are roughly arranged in obliquely transverse rows, with the smaller cerata located anteriorly, ventro-laterally, and posteriorly, a typical arrangement in this Opisthobranch group. The cerata number increases with size of individual, but the usual number is from 8 to 15 oblique rows, with two, three, or even four cerata in each row. A 10 mm. long mature specimen may have only about 16 cerata on each side, while a large specimen may have about 40, including many very small ones. In life the cerata are spindle shaped, abruptly widening close to the base and tapering distally toward the blunt point (figure 7). The side held against the back and against other cerata is somewhat flattened so that the larger cerata, about 2 to $2\frac{1}{2}$ mm. long, are ovoid in cross section and may be somewhat flattened toward the ends. In preserved material the cerata seldom retain life-like proportions; they usually change to a slender, evenly tapering form, circular in cross section. In life the cerata are contractile, with well-developed longitudinal muscle strands arranged in a loose cylinder around the digestive diverticulum (see figure 7 B).

The cerata tips are light in color, usually creamy-white while the lateral cerata surface, that usually exposed to view, is black. Lightly pigmented cerata show minute white dots, especially clustered at the tip (figure 7 B); these can be identified in sections as large mucus gland cells. The proximal half of the inner, hidden surface (figure 7A) is creamy-white and shows the dendritic pattern of vessels as described for Hermaeina orientalis, H. nigra, and H. toyamana by Baba (1949, 1959). These veins are not easily seen in preserved material and may also be difficult to detect in many lightly pigmented live animals.

Other structures visible on the dorsal surface are the very slightly elevated anus, located just to the right of midline, near the second and third cerata, a black spot near it, and the renal aperture. In intensely pigmented individuals, the back is solid black, and these structures cannot readily be found. In many animals the black pigment of the back is broken up by irregular unpigmented streaks, and in these, a clear area is usually present around the anus and the renal pore. The black spot seen near the anus is the location, just under the surface, of a small vesicle which has an intensely pigmented wall and a short duct opening to the surface well away from the anus so that this structure could not contribute a solidifying secretion to the feces. The renal aperture is tiny but can often be located in the center of a clear spot to the right of the heart area at the level of the fifth or sixth cerata row (figure 1).

The foot is prolonged posteriorly so that it extends behind as a slender tail (figure 1). It is widest anteriorly, and this end often shows slight bilobation in a crawling animal (figure 2) (see description of feeding). The anterior end of the foot projects forward under the head and between this anterior margin of the foot and the head above is a shallow median pit. Into this pit above the end of the foot opens a large number of small whitish foot glands (figure 4 fg). In the living animal the foot is not sharply set off from the sides by any groove or ridge but rather by color. The foot is much lighter than the sides. The foot margin is often a pure cream color, while the center of the sole is usually streaked and marbled by black pigment

(figure 2). This is quite variable; in a few individuals the s o l e was virtually pure cream color, but in most there is some streaking vaguely arranged into two parallel longitudinal bands down the foot reminiscent of the b o l d pattern on the foot of Hermaeina minor (Baba, 1959).

The non-pigmented areas of the head produce a characteristic "masked" pattern. Dorsally, the eyes are surrounded by ovoid clear areas, and this zone extends anteriorly up along the lateral edges of the rhinophores (set off by dotted lines in figure 1). Paralleling this is a similar non-pigmented s t r i p on the anterior rhinophore edge, leaving a black strip running up the middle. This black strip widens across the width of the rhinophore near the tip, which is cream colored. The trough-like underside of the rhinophore is not pigmented. The width of the rhinophore is c o n s t a n t almost to the rounded tip.

The rhinophores are auriculate, with both the median a n d the lateral borders rolled in slightly toward the middle. These margins are mobile and may be unrolled and the flat surface presented anteriorly. The antero-median bor-
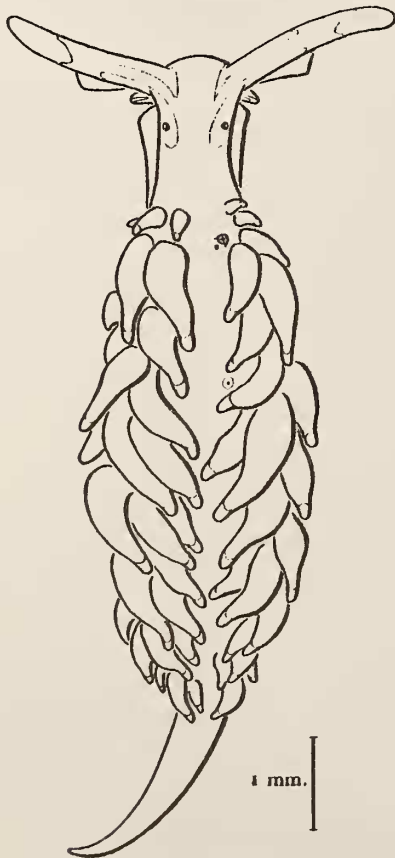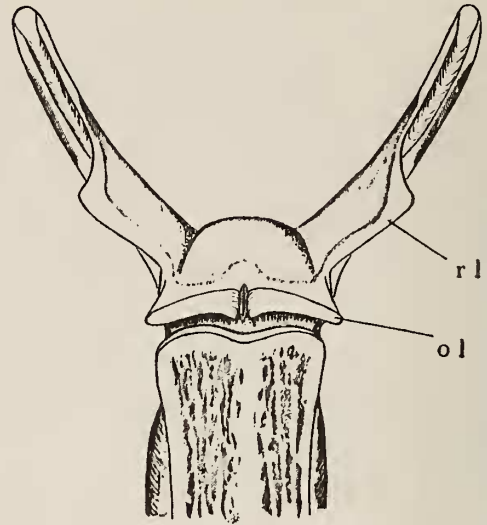

Figure 2: Ventral view of head of living animal (black pigment shaded)

r l - rhinophoral lobe
o l - oral lobe

der is extended as a rhinophoral lobe (figure 2, r l) about one-third of its l e n g t h from the base. This extension is folded across the rhinophore a n d extends past the postero-lateral border so that it is visible dorsally (see figure 1).

The m o u t h is directed downward on the ventral surface of the head. It is flanked by two highly mobile lips, or oral lobes (figure 2, or l), which extend tab-like from near the rhinophore b a s e s downward. These oral lobes are usually extended downward as in figure 2 and are repeatedly touched to the substrate as the animal crawls. The lobes are extended directly anterior a n d their median edges incurved in feeding (figure 3). The sides of the lobes are cream colored, usually with a median black streak down their length. Their ventral edges and part of their anterior faces are also cream colored, while their posterior faces are black. The ventral surface of the head t h u s displays an unpigmented pattern extending onto the rhinophore lobes, around the mouth, and on the oral lobes, which is indicated in figure 2.

Feeding

The animals crawl onto an algal filament and, grasping it with the anterior margin of the foot and the oral lobes, begin to feed (figure 3). No sticky secretion, such as observed by Fretter (1941) in feeding E l y s i a, was seen. The oral lobes are extended anteriorly and their inner margins clasped across the filament. The

1 mm.

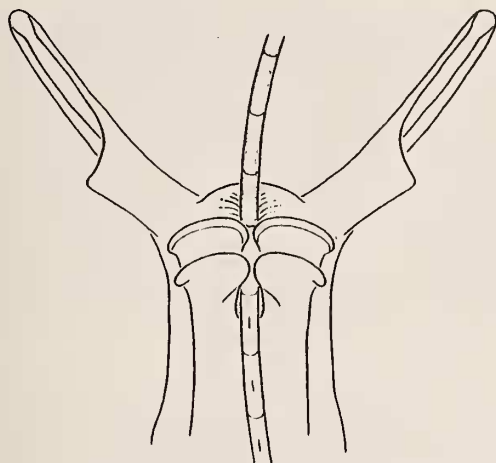Figure 1: Dorsal view of living animal, crawling

Figure 3:　Ventral view of head of feeding animal
(note slits in cells)

anterior margin of the foot is extended in a bi-
lobate fashion and these lobes also grasp the
filament. This holds the filament securely and
bends it in toward the mouth. An algal cell is
slit with the radula and the contents quickly
evacuated; the animal then moves to the next
cell of the filament. The action of the radula
could be seen in animals feeding on Rhizoclo-
nium. The radula is extended outward and
back, pressed against the cell, then pulled in-
ward and forward, producing a fine slit (see
cells in figure 3) in the cell wall. Observation
of details was difficult, but it appeared that
only one tooth was used in the cutting action.

This general mode of feeding is the typical
sacoglossan method and has been previously
described by Rao (1937) for Stiliger gopalai, by
Fretter (1941) and MacNae (1954) for Elysia,
by Gascoigne (1956) for Limapontiids, and by
Gonor (1961) for Lobiger serradifalci. In addi-
tion, both MacNae and Gascoigne observed a
grasping action of the foot margin and the lat-
eral lips similar to that described here.

Internal Anatomy

Features of external form and color serve
to differentiate species of Sacoglossa, although
sometimes imperfectly, but are of little aid in
grouping species or understanding relations
within the group. The major features of inter-
nal anatomy are given here as an effort toward
these ends. Both dissections and serial sec-
tions were examined, but histology will not be
given except where necessary.

Figure 4, a ventral view of a dissection,
indicates the topographic relations of the major
internal structures. In this figure the gonad is
displaced to the right and many of the fine tu-

bules of the albumen gland are removed.

The slit-like mouth was described above.
In dissections the stout buccal bulb (figures 4,
5, and 6) can be seen to be surrounded at its
oral end by a mass of small bulbular multicel-
lular buccal glands (figures 4, 5, b g) with
short necks that open ventrally into the oral
cavity. The buccal bulb is lined inside by a
smooth cuticle. The muscle of its wall is not
striated as is that of Hermaea dendridica
(Fretter, 1941). From the side and ventral view
the well-developed ascus (figure 5, as, figure
4) can be seen to be almost as large as the buc-
cal mass proper. The posterior edge of the
ascus is keel-like so that the posterior end ap-
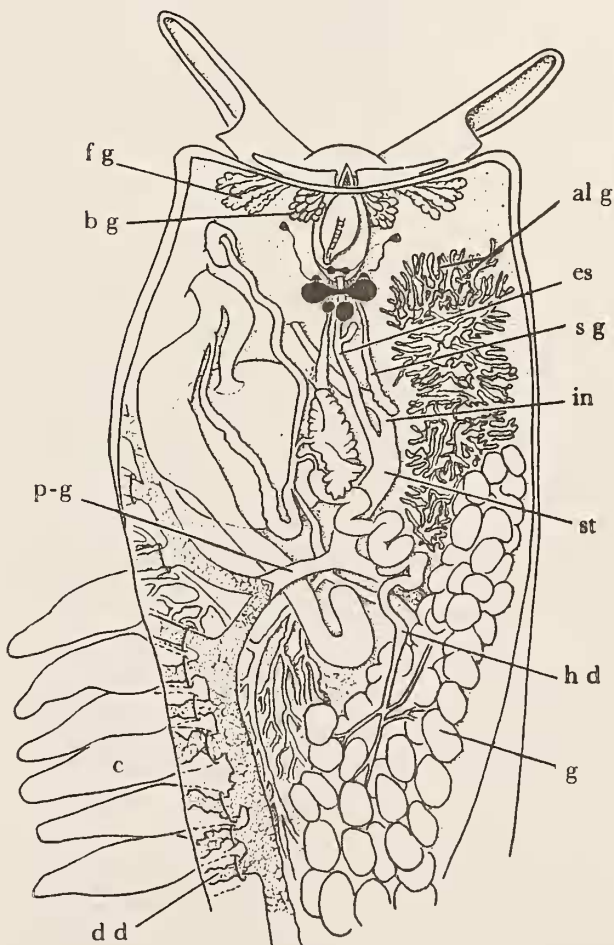pears pointed. There are a pair of stomato-

Figure 4:　Dissection, ventral view

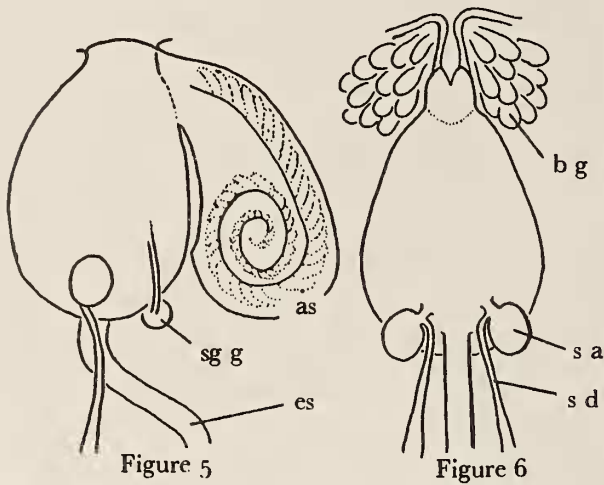| al g | - | albumen gland | s g | - | salivary gland |
es	-	esophagus	f g	-	foot glands
in	-	intestine	b g	-	buccal glands
st	-	stomach	d d	-	digestive diverticulum in a
h d	-	hermaphroditic duct	c	-	ceras
g	-	gonad	p-g	-	pre-glandular portion
					of digestive diverticulum

Figure 5:   Lateral view of Buccal bulb

as - ascus
sg g - stomatogastric ganglion
es - esophagus

Figure 6:   Dorsal view of Buccal bulb

b g - buccal glands
s a - salivary ampulla
s d - salivary duct

gastric ganglia (figure 5, sg g) closely attached to the posterior and ventral surface of the buccal mass. Two slender salivary glands (figure 4, s g) extend from the posterior end of the buccal mass, near the esophagus, through the nerve ring. They widen posteriorly but remain strap-like and do not branch. The ciliated salivary ducts (figure 6, s d) do not directly enter the bulb but on its dorsal surface join the very short ducts of two small, rounded vesicles, or salivary ampullae (figure 6, s a) with thin, muscular walls. These salivary ampullae are apparently reservoirs which can forcibly eject their contents into the posterior parts of the buccal bulb. Cyerce elegans has a similar arrangement of salivary glands and ampullae (Hoffmann, 1938, p. 1065), and Limapontia has similar salivary vesicles on the salivary duct itself (Gascoigne, 1956).

The long and slender esophagus arises dorsally from the buccal bulb (figures 4, 5, es) and extends posteriorly for about one-fourth the length of the animal before joining the Y-shaped stomach area near the place where the intestine (figure 4, in) leaves it. About midway along the length of the esophagus is located a small diverticulum (see figure 4) which extends antero-dorsally. Its structure is not different from that of the rest of the esophagus. The stomach area gives rise to two nonglandular arms (figure 4, p-g, preglandular portion

of digestive glands) extending laterally, each to bifurcate into an anterior and posterior extension of the brown digestive gland, running dorsally under the cerata rows. The digestive diverticula (figure 4, d d) come off from these extensions and run into the cerata (figure 4, c) where they are moderately lobate or branched (figure 7B). The diverticula narrow as they pass through the body wall, and there is present here a sphincter reminiscent of that described by Marcus (1959) for the same situation in Hermaeina brattstroemi.

The intestine runs antero-dorsally from the stomach to open as the anus dorsally, and just to the right of the midline, posterior to the level of the first few cerata. The lining epithelium of the intestine is ciliated and thrown into folds but is nonglandular, unlike that of Hermaea dendridica (Fretter, 1941).

The older portion of the radular ribbon retains its organization and can be seen coiled in the ascus, making up to three turns (figure 5, as). As the ribbon moves into the ascus a cuticular membrane is laid down around it so that the radula is enclosed within a very thin, tubular casing, indicated in figure 8C. This casing does not dissolve in potassium hydroxide and can be seen in radular preparations, rather closely applied to the teeth. The figure of the radula of Phyllobranchopsis enteromorphae given by Cockerell and Eliot (1905) shows a similar membrane. The coiling of the old portion of the radula is not simply due to the rib-

Figure 7:   Cerata
A   Median side, appearanc of surface in life
B   Median side, internal structure

bon being mechanically forced into the confines of the ascus. Radulae isolated from both fresh and preserved material by maceration in a weak detergent solution and freed from all tissue and membranes still exhibit coiling. All parts of these radulae are very springy and recoil tightly when straightened with needles. The coiling seems inherent in the basal ribbon for the ascending arm of the radula, not yet coiled in the ascus and held almost straight by tissue, also bends into a tight curve when freed from the tissue.

The number of teeth varies with the size of individual. Most local animals are about 10 mm. long and have tooth numbers ranging from 33 to 49, but a large specimen had a radula of 88 teeth. These numbers include the first four or five teeth, which are very small and rudimentary, consisting mostly of the flat basal portion. The maximum length of unused teeth in the usual radulae varied from 125 to 170 microns.

The base of the radular tooth is rectangular, with thickened lateral edges and a slightly excavated surface attached to the basal ribbon. From the base rises the crown or middle portion of the tooth, which is thickened down the center. The middle portion bears distally the rounded tooth tip, a very thin, discoidal lamina which is the principal cutting portion, judging from the extensive wear it shows in old teeth. The middle portion of the tooth bears, on its leading (cutting) edge, two serrate lamina flanking a longitudinal excavation in the face of the tooth into which fits a humped keel on the back of the preceding tooth in the series. The sharply pointed denticulations of the serrate edge are directed slightly inward. They show only occasional wear in old teeth. These denticulations are tallest in the center of the laminae and evenly spaced. Near the middle of the largest teeth the denticulations are about 2.5 to 3 microns high and spaced about 5 or 6 teeth per 10 microns of lamina edge, with 2 micron spaces between their tips. This is twice the number given by Marcus for denticles in the type specimen, otherwise his description and figure is identical to the one here. However, a radula with 50 teeth, from a 7.5 mm. long (live) specimen from La Jolla, California, had 3 denticulations per 10 microns of edge at midlength of the serrate lamina, in teeth 150 microns long, corresponding to the figure of Marcus (1961) for the type specimen. A specimen from the type locality (Tomales Bay) 11 mm. long (preserved) with a radula of 40 teeth had 3

to 4 denticles per 10 microns length in teeth 170 microns in heighth. Differences between other details of the teeth of the California material and the teeth of the Washington material are no greater than differences between teeth in the same radula or between two Washington individuals. This minute difference is the only one noted between the morphology of California specimens and local ones and is not considered of specific importance.

The predominant feature of the back of the tooth is a large median humped ridge, slightly excavated at the sides, with a rounded edge. Distally, between this ridge and the tooth tip is a prominent indentation into which fits the tip of the succeeding tooth. There is a pair of low laminae running on either side of the large median keel, which start as faint lines near the middle of the ridge and rise slowly as they proceed distally. They are widest on either side of the indentation in the tooth back and end on the tooth tip. The denticulate edges of the succeeding tooth fit closely inside these laminae, further interlocking the teeth. The close interlocking of the teeth and the tension of the basal ribbon would seem to afford the necessary rigidity to hold the tooth being used in position while in action.

The cutting tip of the teeth shows marked effects of wear; the thin, broadly ovoid tip of unused teeth wears down so that the used teeth have a truncated end. The teeth within a radula show considerable differences in the amount of wear to which they have been subjected. Smaller and medium sized teeth are relatively more severely worn down than larger ones in the same radula, and the cutting edge of some of the smaller teeth may be completely worn off. Comparison of large and small radulae reveals the same type of difference between teeth in analogous positions. Figure 8 demonstrates the differences between unused (A, A1) and used (B, B1) teeth. The difference between the amount of wear of larger teeth and smaller teeth of the same radula can be seen by comparing A with C, while the comparison of A and A1 indicates the difference between used teeth of small and large radulae, respectively.

The dusky yellow gonad, the largest internal structure, lies ventral to the other viscera (figure 4, g). The gonad is elongate, extending at maximum development from the far posterior limit of the haemocoele at the base of the tail anteriorly to more than three fourths the length of the body. It is composed of many

well separated ovoid lobules which are joined only by ducts. Each lobule produces both eggs and sperm. The small collecting ducts from each lobule join a narrow duct that runs through the center of the gonad. From the latter duct, about at the middle of the gonad, runs the common hermaphroditic d u c t (figures 4, 9, h d). The hermaphroditic duct is narrow at its ori-

gin but quickly enlarges, and the tightly coiled portion is swollen to form a sperm storage organ (ampulla). Shortly before joining the other reproductive structures, t h e hermaphroditic duct again narrows to a fine tube which, like the ampulla region, has a ciliated epithelium, but the muscle layer in its wall is thicker than that in the ampulla. The male portion of the rest of the genital tract will be described first. The vas deferens (or efferent duct) (figure 9, v d) arises from the hermaphroditic duct very near the common junction of the latter and several other structures. The first portion of the vas deferens is a fine tube leading to a yellow, multilobulate prostate gland (figure 9, pr g) w h i c h is appended to the vas deferens by a short duct leading from its cavities. After the junction of the prostate gland and vas deferens, the latter is a larger, ciliated tube with muscular walls. It runs anteriorly to enter the penis (figure 10, v d) without change in structure. The male atrium, or eversible penis sac (figure 10, w p s wall, penis sac) opens to the exterior on the right side, below and just posterior to the level of the eye, as the male aperture. When the penis is extended (figure 9, p)
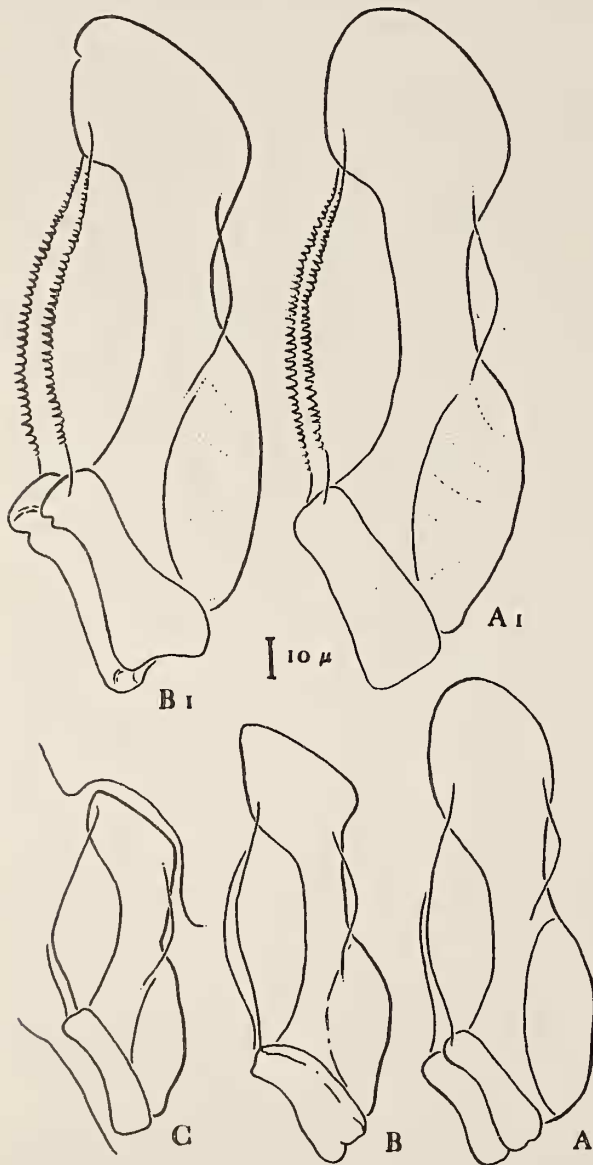

Figure 8:   Teeth from small (A to C)
and large (A1 to B1) radulae
(camera lucida)

A Unused tooth from small radula
B Used tooth, same radula (first preceding tooth in use)
C Used tooth, same radula (9th preceding tooth in use)
A1 Unused tooth from large radula
B1 Used tooth, same radula (first preceding tooth in use)
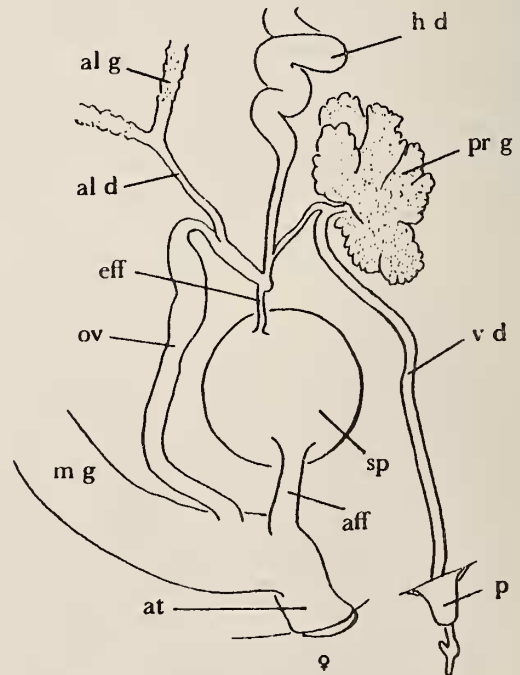
Figure 9:   Genital System (Dissection)

al g	- albumen gland	pr g	- prostate gland
al d	- albumen duct	s	- spermatheca
ov	- oviduct	h d	- hermaphroditic duct
m g	- mucus gland	v d	- vas deferens
aff	- afferent spermathecal duct	p	- penis
eff	- efferent spermathecal duct		

it appears as a cone-shaped base surmounted by the small, unarmed muscular penis proper, which projects straight out. The penis is a barb-shaped structure when everted, with a blunt, tapered tip or penial tentacle (figure 10, t) and a small, blunt backward projecting arm bearing the orifice of the vas deferens (figure 10, o v d). When the penis is retracted the conical penis base is inverted (figure 10, c p b). When the penis is extended, the penial tentacle becomes filled with body fluid and distended straight out (figure 10B). There is a single female orifice (figure 9, ♀) just posterior to the male aperture, rather than separate vaginal and uterine openings. The female orifice leads into a short, wide female atrium (figure 9, at) which is partially partitioned by folds into uterine and nidamental portions. The truly common portion of the atrium is nonglandular and ciliated. Leading from the anterior side of the female atrium is the large ciliated afferent duct (figure 9, aff) of the spermatheca. The spermatheca (figure 9, sp) is a large, spherical brownish organ and, when filled with sperm and secretion of the prostate, may be enormously enlarged and form a bulge in the right side of the body. The epithelium of the spermathecal wall is glandular except for a small area on the postero-ventral portion. Here it is ciliated and in the center of this area is located the opening of a short, thin ciliated duct (figure 9, eff, efferent duct of spermatheca). This duct contains sperm apparently collected from the spermathecal contents. It leads to the area of junction of the albumen gland duct (figure 9, al d), the distal oviduct (figure 9, ov), and the hermaphroditic duct (figure 9, h d). This is probably the site of fertilization. This common female section is ciliated and has a thick muscular wall, which could act as a valve to regulate the entry of eggs from the hermaphroditic duct and exclude the animal's own sperm. The ciliated nonglandular albumen duct and an efferent oviduct are connected near each other, at the posterior end of the chamber, opposite to the hermaphroditic duct. The albumen duct extends posteriorly a short distance, where it receives at once the two branches of the albumen gland (figure 9, al g). The albumen gland is a very extensive structure (figure 4, al g), apparently basically composed of two bilateral portions which ramify and branch so extensively that they cannot be separated except at their junctions with the common albumen duct. The extensive dendritic branches of the albumen gland are mostly located dorsally and to the sides, under the heart and kidney but above the other structures. The
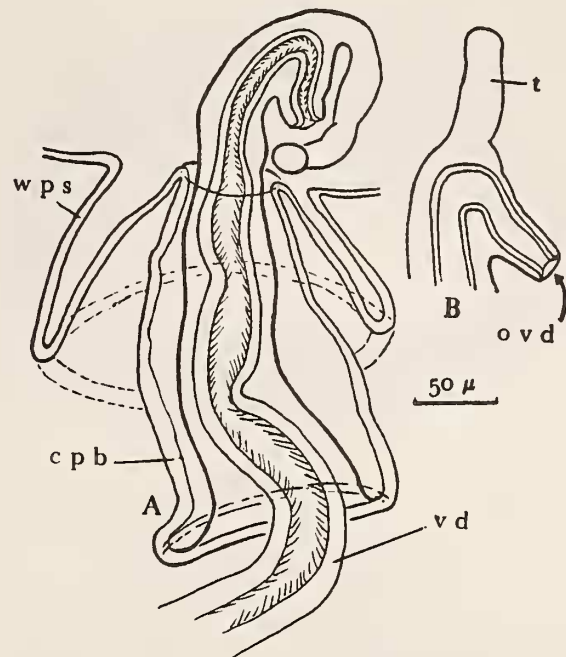

Figure 10: Penis and duct
(total preparation, camera lucida)
A Completely retracted penis
B End of penis, extended state

w p s - wall of penis sac (male atrium)
c p b - involuted conical penis base
v d - vas deferens
o v d - orifice of vas deferens
t - penial tentacle

fine translucent tan tubules composing the gland extend into all parts of the haemocoele, between the organs, even into the head, but do not enter the cerata or rhinophores.

A large, ciliated oviduct (figure 9, ov) leaves the common female chamber and runs anteriorly toward the female atrium on the right. A short portion of its end connected to the chamber is muscular, while most of its length contains mucus gland cells. The oviduct joins the large, pale yellow mucus gland (figure 9, m g) just posterior to the junction of the latter with the female atrium. The oviduct opens into the base of a crease in the wall of the mucus gland which runs in the median side of that gland posteriorly to its tip. This crease partially partitions off a nonglandular ciliated track of the mucus gland in a manner strikingly similar to the way the mucus gland of bulloid tectibranchs is partitioned. Figure 11 depicts a diagrammatic transverse section of the mucus gland. Apparently eggs are carried in this ascending groove (figure 11, asc) to the tip of the gland, and then pass back down anteriorly
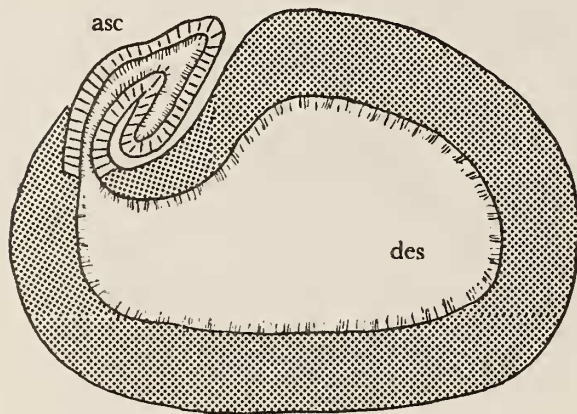
Figure 11:   Diagram of transverse section of
mucus gland   (mucus cells indicated by shading)

asc - ascending ciliated channel
des - descending channel

through the descending glandular section (figure 11, des), propelled by the heavy ciliation of the latter region, to emerge from the female aperture enclosed in the mucus layers of the egg mass.

Individuals spawn repeatedly in the laboratory, attaching the egg masses to any of the algae in the Enteromorpha mat as in the field but also to the sides of the containers. The egg masses are elongate, flattened ribbons, usually about 12 to 20 mm. long, attached by one flat side and usually curved into a "C" shape. They are about 1.5 mm. wide, the width of about 20 egg capsules and about one-half as deep. The closely packed eggs are lemon-yellow when laid, later becoming paler as development proceeds. They are very much like the egg masses described for many other Sacoglossans (see Rao, 1937; Rasmussen, 1951; Baba and Hamatani, 1952; and Hamatani, 1960), and for that reason they are not described in detail or figured here. The larvae emerge as free-swimming veligers and do not settle in dishes in the laboratory, so apparently have a long planktonic feeding phase.

The relative size and position of the ganglia of the central nervous system is frequently of use in comparing different species of opisthobranchs and in assessing relationships. To provide information for this purpose, a brief description of the ganglia will be given here, omitting all considerations of the nerves arising from them. The nerves are largely omitted in figures 12 and 13 for clarity. The terminology used is that of Russell (1929).

The cerebropleural ganglia (figure 12, cp) are ovoid as seen from above, with their long axes running antero-posteriorly. The pedal ganglia (figure 12, pe) are also ovoid, but their long axes are at right angles to those of the pair above. The cerebropleurals extend anteriorly a little further than the pedals, and both pairs of ganglia are well separated, joined by distinct commissures so that they lie to either side rather than directly above and below the esophagus. The connectives joining the cerebropleurals to the pedals are quite short and broad. The statocysts (figure 13, st) are located on the posterior ventral surface of the pedals and project above that surface. The stomatogastric ganglia (figure 5, sg g) are not closely united to the cerebropleurals but joined to them by a commissure as in Elysia.

On the left side a small sub-intestinal ganglion (figure 12, sbi) can be seen between the left cerebropleural and the large abdominal ganglion, joined to each by a short connective. The abdominal ganglion (figure 12, ab) is only slightly smaller than the pedal ganglion. It is displaced somewhat to the left of midline. On the right the supraintestinal ganglion (figure 12, su-i) can be seen to be joined to the right cerebropleural and to the abdominal by short, equal connectives. The supraintestinal ganglion has appended to it a small satellite ganglion (figure 12, sat) of undetermined homology, which in part may represent the right parietal
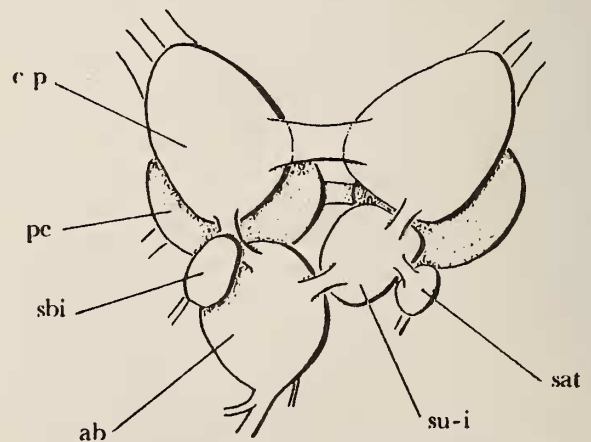

Figure 12:   Central nervous system, dorsal view
(total preparation, camera lucida)

cp - cerebropleural ganglion
pe - pedal ganglion
sbi - sub-intestinal ganglion
ab - abdominal ganglion
su-i - supra-intestinal ganglion
sat - satellite ganglion

ganglion of the tectibranchs. It gives rise to a single small nerve that runs directly posterior but which could not be traced to its ending.

In general, the central nervous system of this species is notable for the lack of fusion and the distinctiveness of the ganglia. Except for the small satellite on the supraintestinal, it is remarkably like the nervous system of Elysia viridis described by Russell (1929). It differs from that of Stiliger gopalai (Rao, 1937, textfig. 1) and other Stiliger species (Hoffmann, 1936, p. 757) as well as from Hermaea dendritica (Hoffmann, 1936, p. 755, Fig. 530C, from Vayssière, 1888), in that the small sub-intestinal ganglion is distinct and not fused into the abdominal. Apparently this fusion has occurred independently several times in the Sacoglossan group, since the seven ganglia are distinct in otherwise diverse forms such as Elysia viridis (Russell, 1929), Cyerce iheringi (= Lobifera crystallina) (Pelseneer, 1894), Oxynoe olivacea (Hoffmann, 1936, p. 756), and in the present case.

The pericardial bulge is not prominent on the dorsal surface but low and gently rising. The pericardial cavity and heart are, however, large, occupying the middle of the dorsal surface starting at a point about one-third of the body length from the head, just anterior to the renal pore. The kidney is an extensive flat sac extending under most of the dorsal surface, lying just under the dorsal epithelium but not applied to it. Its walls consist of a simple, nonfolded epithelium. The anterior end of the kidney is at the level where the intestine emerges from the stomach. It is narrow and mid-dorsal here; posteriorly it widens, and in front of the pericardial cavity it extends across the width
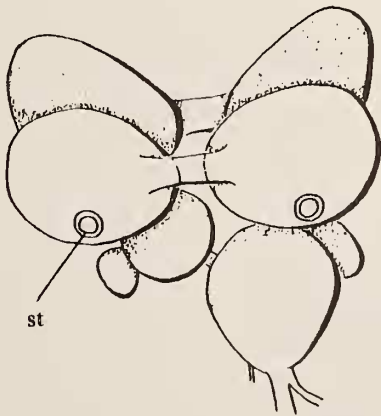

Figure 13: Ventral view of central nervous system (camera lucida)

st - statocyst on pedal ganglion

of the back. It is narrow at the level of the heart, placed almost completely to the right of the pericardial cavity but overlaps it slightly. The renal pore leads from the anterior part of the narrowed portion. More posteriorly, where the kidney is closely applied to the side and part of the dorsal surface of the pericardial membrane, is found the renopericardial aperture. The kidney is widened and again mid-dorsal behind the heart. It narrows and ends just anterior to the tail region. The kidney, in partially surrounding the heart, resembles that of Stiliger gopalai (Rao, 1937) but is more extensive anteriorly than in that species.

Discussion

Ecology: The habitat of this species on the coast of California and Washington was discussed earlier. It is becoming firmly established that the Sacoglossa are typically restricted, as it has been shown here for Hermaeina smithi, in habitat and feeding to one or a few closely related species of algae. MacNae (1954) has discussed the association of many Elysia species with Codium (Siphonales); Gascoigne (1956) has established experimentally that two species of Limapontiids are restricted to Cladophora species, while a third is restricted to Vaucheria (Siphonales); Rao (1937) found that Stiliger gopalai will feed only on Chaetomorpha; and Gonor (1961) has reviewed the association of the Oxynoids with Caulerpa species (Siphonales). This type of information can greatly aid faunistic and zoogeographical investigations and may in time, through clarifying ecological specializations, assist in the understanding of the interrelationships within the Sacoglossa. For example, knowledge of the relation of Bosellia mimetica, a cryptic species, with the alga Halimeda tuna (Siphonales) enabled Portmann (1958a, 1958b) to rediscover this form and greatly extend its known range; and the association of the Tamanovalvidae with Caulerpa species has permitted the collection of this very interesting group in Australia (Burn, 1960a, 1960b) and Baja California (Smith, 1961). The constancy of such associations is borne out by the findings of Marcus and Marcus (1956) and Hand and Steinberg (1955) which demonstrate that Alderia uda and the well known Alderia modesta occupy identical habitats (mud flats, on Vaucheria) in widely separated parts of the range of this genus (Europe, Brazil, California, and Washington).

Systematics: Ten species of the genus

Hermaeina have been described to date; these are:

1. Hermaeina maculata Trinchese, 1874; from the west Mediterranean coast of Europe.
2. H. (Phyllobranchopsis) enteromorphae (Cockerell and Eliot, 1905); from San Pedro, California.
3. H. orientalis Baba, 1949; from Sagami and Suruga Bays, Japan.
4. H. nigra Baba, 1949; from Sagami and Toyama Bays, Japan.
5. H. formosae Pruvot-Fol, 1953; from the Atlantic coast of Morocco, North Africa.
6. H. sinusmensalis MacNae, 1954; from Table Bay, near Capetown, South Africa.
7. H. minor Baba, 1959; from Toyama Bay, Japan.
8. H. toyamana Baba, 1959; from Toyama Bay, Japan.
9. H. brattstroemii Marcus, 1959; from Northern Chile.
10. H. smithi Marcus, 1961; described from Tomales Bay, California.

With the possible exception of the first, none of these species has been described in sufficient detail to be distinguished completely and with certainty from all of the others, yet the resemblances are such that at least some are probably synonymous. All lots of material examined in this study agreed in the details of internal anatomy, especially the genital system, so these species will be discussed in the light of the variation shown to exist in the external appearance of Hermaeina smithi. It is probable that the material described by Eliot (in Cockerell and Eliot, 1905) was of the species treated here; this, however, cannot be established definitely, and it seems best to regard this name as a nomen dubium. Eliot carefully stressed in three places that his four specimens were badly macerated both externally and internally and that important distinguishing characters could not be made out with certainty. The only character that might allow identification is the description that the cerata were flattened. Their shape was not further described, and the very poor figure is useless. The abundant material examined here occasionally showed flattened cerata tips, and in badly preserved specimens other distortions as well, and it seems likely that material in the condition described by Eliot would be likewise distorted. Moreover, in starved animals the cerata become more flattened and ovoid as the digestive diverticula regress. The figure given by Eliot of the radula is obviously of a Hermaeina, but it is of the worn portion only and cannot be used to distinguish the species.

The other species from this Pacific coast, Hermaeina brattstroemi, was also described from a single small preserved specimen, and unfortunately, much of its anatomy is unknown, since it was sexually immature. It cannot be completely distinguished from the present material on external appearance. Contracted, preserved specimens of H. smithi often resemble the figures Marcus (1959, figs. 21-23, p. 113) has given, in that the cerata and the labial lobes may be much contracted and the rhinophores very shortened so that their natural shape is lost; they come to be short and widened distally, with the rhinophoral lobe quite obscure. The foot is identical, and the range of variation in pigment intensity and pattern include the condition of Marcus' specimen. The careful drawing of two apparently unused radular teeth (Marcus, 1959, fig. 27, p. 114) does not show any features which would distinguish these teeth from some of the material examined in this study, and indeed resembles the figure later provided for H. smithi. However, Marcus states that the earlier teeth were not in order in the ascus, a feature not shown by any of the other known species. Two other features might distinguish this southern form. Figure 24, p. 113, of Marcus (1959) indicates that the digestive diverticula only bulge out at regular intervals. In the present material these structures varied from showing slight, irregular lobulation in young and starved animals to extensive, rather regular branching of the type indicated by fig. 34, Pl. 2 of Marcus, 1961. The penis described for the specimen of H. brattstroemi consisted of a simple straight tubular structure. If this organ was completely differentiated in this immature specimen, then it alone will serve to differentiate the two species.

Hermaeina sinusmensalis MacNae was not sufficiently described to permit it to be distinguished from other dark species with any certainty. The description of the radula permits assignment to the genus only; it is presumed that the structure of the teeth was misinterpreted because of the close overlapping and that they are similar in detail to those of other species, with two denticulate lamellae on the cutting face. Unfortunately, the size and shape of the terminal disc cannot be used alone as a specific character because it is subject to wear; indeed, it differs slightly within the unused teeth of the same radula in H. smithi.

The material examined is identified as Hermaeina smithi chiefly on the basis of the morphology of the penis as given by Marcus (1961) since this proved to be completely con-

stant while other characters given proved to be quite variable or of generic level only. The form of this structure is usually species-specific in Opisthobranchs and is used here in selecting a name for the material studied even though the structure is not described for most of the species.

It is difficult to evaluate the four species described from Japan by Baba, since he provided no information about internal anatomy. Fortunately, however, Baba was able to examine and accurately figure living material. All four species show certain close resemblances to the present material, at least indicating that this genus is a well defined group of closely related species and further emphasizing the marine faunal connections between Japan and the American Pacific Coast (Baba, 1957; Marcus, 1961). These common characters have been utilized in an attempt to re-define the generic concept.

The two light-colored species of Baba seem distinct from Hermaeina smithi. Hermaeina orientalis has strongly rolled rhinophores with flaring tips and no rhinophoral lobes, thus differing from H. smithi. The black-tipped cerata seem more pointed as well. Baba only tentatively separated the other light form, H. toyamana, from H. orientalis because of difference in pigment intensity, and it is likely that these specific names are synonyms.

Because of the highly variable nature of the black color and the variation in tooth and cerata number with age and size, it is more difficult to separate Hermaeina smithi from the two black Japanese species, H. nigra and H. minor. According to the very brief description, H. minor differs from the preceding two in that it is said to have no ceratal veins and, judging from the figure (Baba, 1959, figs. 7, 7a), apparently no rhinophoral lobes on the anterior rhinophore margins. The description of H. nigra greatly resembles the specimens of H. smithi in external appearance, except that the three specimens upon which H. nigra was based were larger (12-30 mm. long) and had more ceratal rows (25). The figure (Baba, 1949, p. 34, textfig. 23-B) of an apparently unused radular tooth of H. nigra differs from the appearance of the unused teeth of H. smithi in outline of the tooth tip and in relative height and may prove significant if constant.

The original description of Hermaeina formosa is not available to me at present, but apparently this species is similar to H. maculata in the distinctive color stripes on the cerata

and also in the structure of the radula (Pruvot-Fol, 1954, p. 190). These purple stripes differentiate these two species from H. smithi and the other known Pacific forms.

The two earlier attempts of MacNae (1954) and Pruvot-Fol (1954) at defining the generic concept uniting the species described under Hermaeina may be extended now that more information is available.

<center>Hermaeina Trinchese 1874
Type: Hermaeina maculata Trinchese, 1874
(? = Aplysiopsys elegans Deshayes, 1834-1858)</center>

Rhinophores auriculate, with the anterior (median) border often prolonged into a rhinophoral lobe which overlaps the posterior border below. Distinct, short oral lobes present. Anterior free margin of the foot set off by a groove behind the oral lobes. Cerata fusiform, ovoid in cross section, usually with venation on the mesial surface, and branched hepatic diverticulum (but no branches of the albumen or prostate glands) within. Anus anterior near the first cerata and placed medially, or slightly to the right. The radula coiled in the ascus, with old teeth in order; tooth form (described earlier) quite characteristic of the genus, but not at the specific level. Genital system diaulic, penis unarmed. Often with black or brown pigmentation showing a general pattern, such as clear areas around the eyes and two streaks down the foot, which, however, is held in common with other Styligerids.

Hermaeina may be separated from the genera of the "family" Polybranchiidae (sensus Pruvot-Fol, 1954) possessing cerata on many points of internal and external anatomy. The most important of these are the dorso-median anus, cerata with hepatic branches, unbranched rhinophores, lack of a muscular crop or a large esophageal diverticulum and various details of the genital tract (compare Caliphylla mediterranea, Marcus, 1958) such as lack of peneal style and the single spermatheca.

The arrangement of the supraspecific categories in the Styligerid group is highly artificial and remains in a confused state uninfluenced by evolutionary concepts or newer taxonomic ideas reflected in the systematics of better known groups. This can readily be attributed to the lack of good studies of anatomy. The resulting disorder is well described by Pruvot-Fol (1954, pp. 180 ff.). This situation makes systematic comparison of the genera impossible since they are poorly defined. A

few comparisons have been made in the descriptions of internal anatomy whenever these have been pertinent. Some remarks, supporting the separate status of Hermaeina, about the critical genital system may be made since through the careful work of Marcus and Rao there are available recent accounts of five species of Stiliger (s. s.) and one of Hermaea coirala.

The genital systems of Hermaeina smithi and Hermaea coirala are similar since both are diaulic, with an unarmed penis. But Hermaea coirala has both a spermatocyst and a spermatheca and the latter structure does not have separate efferent and afferent ducts as does Hermaeina smithi. Hermaea dendritica differs even more in that it is triaulic, possesses a peneal stylet and has branches of the albumen gland in the cerata. The reproductive system of Hermaeina smithi differs from this system in Stiliger talis, S. fuscatus, and S. vanellus mainly in that these species are triaulic, have peneal stylets, and the albumen gland joins the mucus gland directly. But in addition, it differs from S. talis and S. gopalai in the location of connections of the female organs.

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On Certain Littoral Species of *Octolasmis* (Cirripedia, Thoracica) Symbiotic with

Decapod Crustacea from Australia, Hawaii, and Japan

by

WILLIAM A. NEWMAN

Department of Zoology, University of California, Berkeley 4, California

(Plates 21, 22, and 23)

This paper concerns the reinstatement of *Octolasmis neptuni* (MacDonald), long held in synonymy with *O. lowei* (Darwin). Australian and Japanese subspecies are designated. The paper is also concerned with a remarkable new species of *Octolasmis* from Hawaii. An analysis of the ontogeny and adult morphology suggests a new interpretation of the origin and phylogeny of this and related forms is required.

POECILASMATIDAE NILSSON-CANTELL, 1921

[TRILASMATIDAE NILSSON-CANTELL, 1934]

Octolasmis GRAY, 1825

Octolasmis PILSBRY, 1907

When Darwin (1851) described the small pedunculate barnacle *Octolasmis lowei* from the gills of a spinous crab from Madeira, he was quite unaware that numerous comparable forms were to be found on large crustacea in all warm seas, and in the depths of the ocean as well. Had he foreseen this, he probably would have recognized that the reduction in external armament of this type of barnacle in response to the protection afforded by the host might not only express more than ordinary variability within a species, but that the trend would achieve comparable degrees and form of disarmament in different species. Had he suspected such trends, he probably would have stressed arthropodal rather than conchological characteristics in the description of *O. lowei* for the future was to see a number of otherwise distinct species confused with it.

Subsequent taxonomists have also tended to rely on conchological characteristics in their diagnoses of species in this group, and many doubtful as well as good species were described during the five or so decades following Darwin.

During this period of expansion, workers began to suspect the sorts of variability found in the group, and many of the previously described species were placed in synonymy. *Octolasmis lowei* acquired ten junior synonyms primarily due to the efforts of Annandale (1909), Barnard (1924), and Nilsson-Cantell (1927). In some cases the synonymies were rather indiscriminately placed, being based on external appearance alone and were thus not well founded (Newman, 1960a).

Resistance to this trend was inaugurated in the brilliant analysis of the "*Octolasmis lowei* complex" by Hiro (1937) in which he clearly demonstrated that the deep water form, *O. aymonini* (Lessona & Tapparone-Canefri), was distinct from the littoral form, *O. lowei* sensu Darwin, and that *O. geryonophila* Pilsbry, also from deep water, was probably closely related to it. He further set order to the complex by dividing the remaining species into two series: forma *lowei* and forma *neptuni*. However, this system has not been followed in later systematic considerations of the group.

I have been able to confirm the opinion of Hiro (1937) regarding the close affinities of *Octolasmis geryonophila* and *O. aymonini*; in fact, it is my opinion that they must be considered the same species (Newman, 1961), It now affords me pleasure to announce that not only is *O. lowei* forma *neptuni* distinct from his forma *lowei* as he proposed, but that *O. neptuni* (MacDonald, 1869), in accordance with the present state of our knowledge, must be considered a distinct species, as originally described. This conclusion has been reached through a study of MacDonald's form from the type locality and type host.

A supplementary description of *Octolasmis*

neptuni is given here, and Australian and Japanese subspecies are designated.

Octolasmis (Octolasmis) neptuni
(MacDonald, 1869)

Distribution: Indo-West-Pacific; Durban, South Africa (Barnard, 1924) and Suez (Gruvel, 1905), to Moreton Bay and Sydney, Australia, and the ? Islands of the South West Pacific (MacDonald, 1869), to the Seto Inland Sea, Japan (Hiro, 1937). ? Caribbean (Pearse, 1932). Occurring on gills, occasionally on mouth parts, of Brachyura, generally portunids.

Diagnosis: Basal segment of scutum narrow, needle-like, usually not reaching carinal fork; tergum broad, semilunar or quadrangular with small occludent projection (Hiro, 1937). Supplementary diagnosis: Basal arm of tergum often chitinous and/or vestigial, situated approximately one fourth the length of the capitulum above the basal fork of the carina. Surface of capitulum and peduncle studded with minute transparent closely spaced sharp or blunt spines (not hair-like bristles or amber beads). Aperture without inner margin of minute denticles. Labrum with 15 to 21 sharp closely spaced teeth; mandible with fifth tooth conspicuous (not rudimentary); penis with apex obliquely truncate, without pronounced apical languet, supporting terminal comb of relatively short bristles; clothed sparsely throughout with soft setae arranged more or less at random or in ill-defined rows.

Octolasmis (Octolasmis) neptuni neptuni
(MacDonald, 1869)

(Plate 21)

1869 Parodolepas neptuni MacDonald: 442
1894 Dichelaspis neptuni (MacDonald), Aurivillius: 19
1900a Dichelaspis vaillanti Gruvel: 2
1900b Dichelaspis vaillanti Gruvel: 109
1900b Dichelaspis neptuni (MacDonald), Gruvel: 110
1905 Dichelaspis neptuni (MacDonald), Gruvel: 127
1905 Dichelaspis vaillanti Gruvel: 128
1906 Dichelaspis vaillanti Gruvel, Annandale: 45
1908 Dichelaspis vaillanti Gruvel, Annandale: pl. 4, fig. 6
1909 Dichelaspis sinuata in part. Annandale: 121 (non D. sinuata Aurivillius, 1894)
1924 Octolasmis neptuni (MacDonald) in part. Barnard: 60
1927 Octolasmis lowei (Darwin) in part. Nilsson-Cantell: 766
1931 Octolasmis lowei (Darwin) in part. Broch: 129
1932 ?Dichelaspis sinuata Aurivillius, Pearse: 110 (identified by P. J. Vissher)
1937 Octolasmis lowei forma neptuni Hiro: 426
1938 Octolasmis lowei (Darwin) in part. Nilsson-Cantell: 11
1960a Octolasmis lowei forma neptuni Hiro, Newman: 108
1960b Octolasmis lowei forma neptuni Hiro, Newman: 10
1961 Octolasmis lowei (Darwin) in part. Causey: 51

Locality: Moreton Bay and Sydney, Australia, on the gills of Neptunus pelagicus (Linnaeus); the islands of the South-West Pacific (according to MacDonald). Eighteen specimens were collected from the gills of N. pelagicus from Moreton Bay, Queensland, Australia, by Dr. Cadet Hand, March 26, 1960. Five of these specimens have been sent to Dr. Huzio Utinomi, Seto Marine Biological Laboratory, Japan.

Neotype: U. S. N. M. Cat. No. 107'011.

Type locality: Moreton Bay; approximately 27° 10' S. Lat., 153° E. Long.

Diagnosis: Capitulum and peduncle translucent, surface studded with minute sharp spines (Plate 21, figure 1). Color (in alcohol), pink. Valves 5 in number; arms not overlapping; basal arm of scutum traversing capitulum approximately one fourth the length of the capitulum above the capitulo-peduncular junction; distal portions of basal arms of scuta and carina chitinous rather than calcareous. Labrum with 15 to 21 closely set minute conical teeth. Rami of Cirrus I equal, each ultimate article supporting 5 or 6 strong plumose spines and a few simple shorter setae (Plate 21, figure 7). Penis with soft setae scattered, or arranged in linear groups of 2, 3, or 4 over the surface; apex without distinct languet, supporting a few short blunt spines and a transverse row of about 7 longer soft setae of about equal length (Plate 21, figure 9).

Supplementary Description: Capitulum ovoid or somewhat pear-shaped, laterally compressed, translucent, tinted pink in most specimens; occludent margin, from basi-scutal angle to apex, nearly straight; orifice somewhat flaring, without inner border of small denticles; carinal margin broadly convex (Plate 21, figures 1, 2). Outline of growth increments as chitinous areas, approximating the original extent of the valves, clearly visible in young spe-

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Explanation of Plate 21

Octolasmis neptuni neptuni (MacDonald, 1869)

Figure 1: neotype; Figure 2: young specimen; Figures 3 through 9: armament and appendages of neotype; Figure 3: spines on peduncle; Figure 4: spines on lateral surface of capitulum; Figure 5: mandible; Figure 6: inner maxilla; Figure 7: last three articles of rami of Cirrus I; Figure 8: caudal appendage; Figure 9: terminal portion of penis.